AGONISTIC INTERACTIONS BETWEEN BLUE-WINGED AND "BREWSTER'S" WARBLERS

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Since the days of Brewster (1881) ornithologists have been intrigued by the relationship between the Blue-winged Warbler (Vermivora pinns), and the Golden-winged Warbler (Vermivora chrysoptera), and their hybrids. There has been a resurgence of interest in recent years, both by systematists (Parkes, 1951; Short, 1963). ethologists (Ficken and Ficken, 1962) and others (Berger, 1958: Gill and Lanyon, 1964). We believe that additional behavioral observations will aid significantly in the solution of the many problems involved in this fascinating complex. From 22 May to 25 June 1961, we spent a total of 25 hours, largely in the early morning, making behavioral observations on two of the forms involved in this complex, a male Blue-winged Warbler and a male "Brewster's" Warbler.

HABITAT DESCRIPTION

The study area was a portion of the Cambridge Reservoir, located largely in Lexington, Middlesex County, Massachusetts (Fig. 1). It may be divided into two major vegetative units; (1) an extensive upland deciduous (oak-hickory) forest. only the southern edge of which was utilized by the "Brewster's" and the Blue-wing, and (2) an abandoned old field or pasture, which had a well-developed peripheral growth of quaking aspen (Populus tremuloides). gray birch (Betula populifolia), black cherry (Prunus serotina), red maple (Acer rnbrum), American elm (Ulmus americana), black locust (Robinia pseudo-acacia), staghorn sumac (Rhns typhina), gray dogwood (Cornns amonum), meadowsweet (Spirea latifolia), catbrier (Smilax sp.), and blackberry (Rubus sp.?). The trees in these stands, which bordered the oak woods and the edge of the reservoir, averaged 20 to 25 feet in height. The central portion had a grassy aspect but was heavily invaded with woody plants. The predominant plant species here were broomsedge (Andropogon scoparius). dewberry (Rubus villosus), goldenrods (Solidago spp.) and asters (Aster spp.). There were several large and many small dead elms, which were frequently used as singing perches.

Areas A and B were essentially in the same stage of development and occupied by the same plant species, but area B had considerably more shrubby growth and less open grassy areas (Fig. 2a and b).

METHODS

We observed the birds with $7\times$ and $12\times$ binoculars. All vocalizations were taped with the use of a Nagra III B tape recorder.

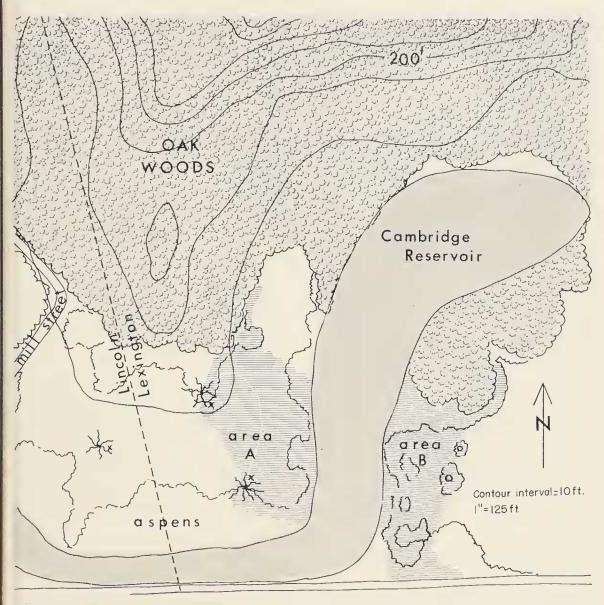


Fig. 1. Map of the study area, part of the Cambridge Reservoir, Lexington, Middle-sex County, Massachusetts. Two circles in area B and X's in area A symbolize prominent song perches (see text for details).

AGONISTIC BEHAVIOR

All of the behavior we observed clearly comes under the rubric of agonistic behavior. Since thorough searches during the entire observation period failed to reveal a single female, we are therefore arbitrarily ruling out sexual motivation. For descriptive purposes, the observed agonistic behavior is classified under three subheads; aerial, non-aerial, and vocalizations. For comparative purposes and where applicable we use the terminology of Ficken (1962a).

Aerial Displays

Diving Attacks.—Of the twelve Diving Attacks seen, all took place in area B,

and eleven were made by the Blue-wing. Diving Attacks typically were launched from a perched position upon either a flying individual or one perched below.

Fights.—Fights were uncommon (we observed six). They consisted of the birds flying up together, briefly meeting in midair, then parting.

Spiralling.—This behavior took place during a chase and began when the birds landed in a small tree or bush. Usually, the uppermost individual hops or makes short flights downward and around the periphery of the tree or bush toward its opponent. Once, however, we saw the lowermost bird spiral upward toward its opponent. Spiralling was observed eleven times and ended when the chase was resumed. In no way does it resemble the Circling of Ficken (1962a).

Supplanting.—Supplanting attacks were observed seven times and in every case they took place during a chase. The "Brewster's" supplanted the Bluewing 5 times and the Blue-wing was the supplanter twice. With one exception, supplanting occurred in Area B.

Chases.—Most of the Chases we saw took place well within Area B, the territory of the "Brewster's" Warbler, and most were initiated by the persistent intrusion of the Blue-wing from Area A. Of the 79 Chases observed, the "Brewster's" was the pursuer in 44. the Blue-wing in 35. Our observations of Chases agree in general with those of Ficken (ibid.) on the American Redstart (Setophaga ruticilla) with respect to ritualization: the pursuer never caught up with the pursued. An even more striking example of the ritualized nature of chases is shown by those involving a display flight, a slower flight than normal (see below). We heard no vocalization, again in general agreement with Ficken (ibid.). Direct. rapid Chases were observed 29 times; all were short and at low level (less than 10 feet). The remaining fifty involved one or both birds in a display flight:

Flutter Flight.—The Flutter Flight display was most often shown after a chase by the bird going away from its opponent. The flight was usually direct, of short duration at low elevation and without vocalizations. The displaying bird held its head high, the feathers of the crown raised, the bill pointed slightly upwards and it occasionally looked to the rear. The tail was elevated slightly above the horizontal, moderately spread and sometimes fanned. The wings were bowed, and the wing tips fluttered (strongly reminiscent of the flight of the Spotted Sandpiper (Actitis macularia) (see Fig. 2a)). The Flutter Flight display, although not exclusively the Blue-wing's display, was more often shown by that individual.

Tail-fanning (aerial).—The Tail-fanning display, shown only by the "Brewster's" was similar to the Flutter Flight except in the following:

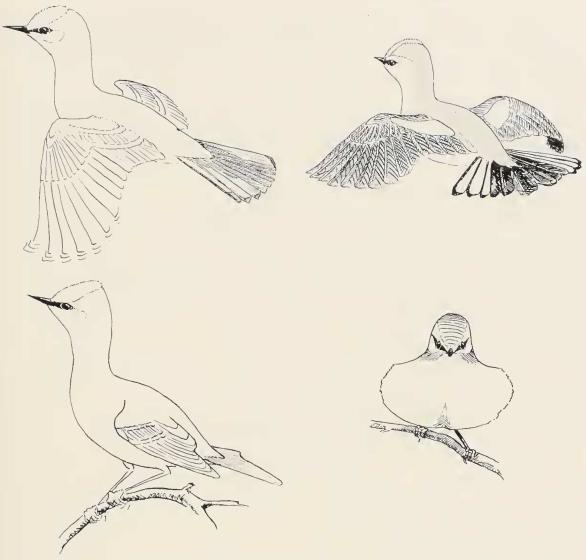


Fig. 2. Aerial and non-aerial displays of the Blue-winged Warbler and the "Brewster's" Warbler. (2a) (upper left) Blue-wing in Flutter Flight Display; (2b) (upper right) "Brewster's" showing Aerial Tail-fanning; (2c) (lower left) Blue-wing in Erect Threat Display; (2d) (lower right) "Brewster's" in Puff Display (see text for details).

(1) the wings were bowed but the wing tips were not fluttered; (2) the wing beats were noticeably slower; (3) the tail was frequently fanned, a movement which made the white tail markings very conspicuous (see Fig. 2b). Occasionally the fanning was extreme.

Non-aerial Displays

Crown-raising.—The "Brewster's" Warbler was twice seen to raise its crown feathers, once in the Puff Display (see beyond) and once as part of a prolonged encounter.

Tail-fanning (perched).—We saw this display given twice by the "Brew-

ster's" and once by the Blue-wing. On each occasion the birds were close to one another. The most extreme fanning (closely approximating the tail spread of the redstart, Ficken (*ibid*.)) was seen as part of the Puff Display (see below).

Erect Threat.—This display was shown only by the Blue-wing. In one instance it raised its head, drooped its wings and quivered them while sidling directly towards the "Brewster's." In the other, it perched erect, with the wings drooped stiffly and the tail partially spread (see Fig. 2c). At first glance, this apears to be the Male Soliciting display described by Ficken and Ficken (ibid.) for the Golden-winged Warbler, but our observations indicate that the context in which the Erect Threat is shown differs from that of Male Soliciting, which Ficken and Ficken state as being an outcome of being "defeated after prolonged boundary conflicts." It is true that this display was shown after prolonged boundary disputes, but the displaying Blue-winged male sidled toward the "Brewster's" Warbler. The display seemed to us to be in the nature of a threat to the "Brewster's" rather than submission following an unsuccessful encounter, since the agonistic interactions were resumed at once after display of the Erect Threat by the Blue-wing. In Male Soliciting, according to the Fickens, the displaying bird faces away from its opponent, signifying submission after losing the boundary encounter.

Puff Display.—This was the most striking non-aerial display we observed. and it was shown only once, by the "Brewster's," as the terminal display in a prolonged agonistic encounter: The "Brewster's" flew up towards the Blue-wing, stopped when he was three feet away, faced the Blue-wing, ruffled his back feathers, lowered them and then showed the Puff Display—

In this display, the "Brewster's" sleeked his body feathers, then fluffed out his breast feathers until he appeared extremely wide; at the same time he raised his crown until he had what appeared to be a long narrow head with a bright yellow cap. His black eye-stripes, bill and eyes contrasted sharply against the yellow and white of the head (Fig. 2d). The tail was fanned to an extreme degree. The bird held this display for several seconds and then moved closer to the Blue-wing, which flew away. Throughout both birds were silent.

Although birds commonly show Head Forward, Gaping. and Wings Out as part of their agonistic repertoire, the two males observed showed none of these displays.

Vocalizations

Singing was a prominent feature of the overall agonistic situation, but other vocalizations were remarkably infrequent. In fact, we heard vocalizations other than songs only twice: once during a spiralling display the Bluewing called *tic* several times, and once during an especially long encounter chip notes were heard.

Both birds sang almost continuously during the early morning hours (when most of our observations took place), and on several occasions we heard singing in the late afternoon and early evening. Singing remained vigorous until, at least. 13 June and the Blue-wing was heard singing several times on 25 June. Throughout this period the song patterns remained the same in both birds; with one exception, there was no change to a "second" song (see below).

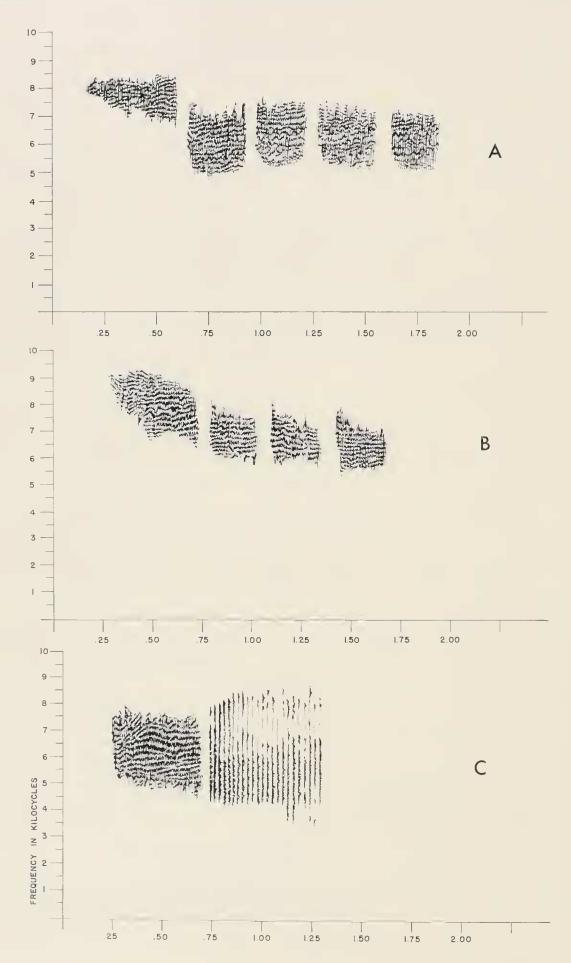
The birds sang most frequently from favored singing perches, which for the "Brewster's" was a small 15-ft. cherry and a similar sized oak in area B (marked with a circle on Fig. 1), while the Blue-wing sang from the upper branches of the many dead elms in area A (marked X on Fig. 1). The Blue-wing did not exhibit as strong a preference for particular singing perches as did the "Brewster's." The birds often engaged in extensive preening while at their singing perches (where they alternately preened and sang), and also sang while feeding but with longer intervals between songs.

As noted above, singing was important in the agonistic interactions between the "Brewster's" and the Blue-wing, and appeared to be an integral part of both the aerial and the non-aerial displays of both birds, as illustrated by the following example from our field notes on 24 May 1961:

0801—Both are singing. Brewster's flies across the clearing, chases Blue-wing; both now at right hand edge of clearing. Brewster's comes back, sits in low dogwood, sings. Blue-wing dives upon Brewster's. Blue-wing singing in top of red maple, Brewster's down low. Both still singing. Blue-wing just flew down to left hand side of clearing where Brewster's is singing. A real song duel going on now. etc.

We recorded 26 instances of what we referred to as "song duels." These took place in a variety of contexts, but were all similar in that they consisted of a song by one bird given in response to a song by the other. Sometimes, these "song duels" took place with the "Brewster's" in area B and the Bluewing in area A, but more frequently "song duels" were part of the general agonistic behavior that occurred whenever the two birds met.

The song of the "Brewster's" was a typical chrysoptera vocalization, beee bzz bzz (Fig. 3, A and B), and was the only song type heard. The Bluewing had two songs, neither of which was a characteristic pinus song type (Fig. 3, C), but were more chrysoptera-like; both were similar in form, differing only in the number of bzzes, and may be phoneticized as beee bzz bzz bzz, or beee bzz bzz bzz, all given on the same pitch (Fig. 3, D and E). This part of New England has long been well known as a zone of hybridization between chrysoptera and pinus, and it is therefore not surprising that the Blue-wing would show some sign that it was not phenotypically "pure,"



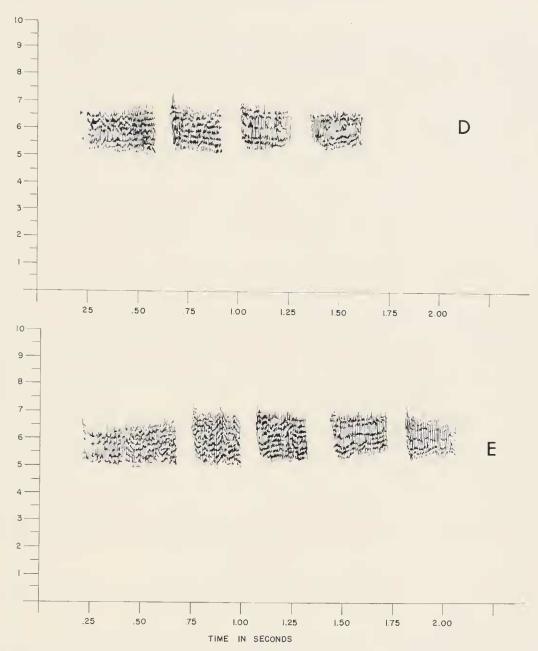


Fig. 3. Tracings of sonograms of the vocalizations of: (A) Golden-winged Warbler—taken from Federation of Ontario Naturalists recording, (B) "Brewster's" Warbler—recorded by the authors in 1961 at the Cambridge Reservoir, Lexington, Massachusetts, (C) Blue-winged Warbler—taken from Federation of Ontario Naturalists recording, (D&E) Blue-winged Warbler recorded by us at the same place and time as B.

although this introgression was not evident in its plumage. The area in which the Blue-wing was found is one where hybridization apparently often occurs,

¹ Although such was our impression, we must qualify this statement by noting that sinee we observed the birds through binoculars and did not examine them in the hand, we eannot state with certainty that the Blue-wing did not show some evidence of introgression in its plumage (cf. Short, 1963 p. 150). The same is essentially true of our observations on the "Brewster's," which resembled, in its general morphological characters, a "typical" "Brewster's" Warbler; we did note that it had a conspicuous yellow wash across the breast.

as shown by the observations of Baird who observed on 16 July 1961, in the then-deserted area A, a *Vermivora* family group composed of a male *chrysoptera*, a female *pinus* and four young—one of which was *chrysoptera*-like and another *pinus*-like, and on 18 May 1962 observed a female "Lawrence's" Warbler with a male *chrysoptera* in a maple swamp less than a mile from the 1961 study area.

Only once was the Blue-wing heard singing a song other than those described above. On 30 May, it sang a single "upward" song which was not heard again. A recording was not made of this song, but it would seem to correspond with the description given by Saunders (1951) for the "second song of the Blue-winged Warbler."

DISCUSSION

Although we were not present when the birds first arrived (the "Brewster's" was first seen by another observer on 14 May), it was our impression that on 22 May both birds were attempting to establish territories in area A (see Fig. 1). Very quickly, however, the "Brewster's" was restricted to area B. In fact, it was not again seen in area A after 23 May, and by the end of our observation period its activities were largely confined to an aspen grove at the south end of B. We believe that this ultimate confinement of the "Brewster's" to a small section of the initially larger area was entirely due to the agressive behavior of the male Blue-wing.

The Blue-wing made constant forays into the "Brewster's" territory (area B); these persistent incursions frequently resulted in prolonged agonistic encounters which lasted from 10 to 37 minutes. These long periods of intense interaction involved almost the entire agonistic repertoire of both birds as observed by us: Pursuit Flights (more than 80), Supplanting Attacks, Fights. Song Duels, etc.

This dominance by the Blue-wing is also indicated by the fact that the Blue-wing often sang from one of the primary song posts of the "Brewster's." Secondly, although the "Brewster's" actively engaged the Blue-wing in aggressive encounters, it never pursued the Blue-wing beyond area B.

Additional suggestive evidence of this Blue-wing dominance is found in the positional relationship of the birds and the number of diving attacks seen. We observed repeatedly, at a ratio of 10 to 1, that during and after prolonged agonistic encounters, the Blue-wing would land higher than the "Brewster's." Although we do not have a clear-cut correlation between height and diving attacks, it is suggested that this might confer an "attack" advantage for the Blue-wing, since it was the attacker in 11 out of the 12 Diving Attacks seen.

As was noted earlier, at no time did we observe any females, and we believe that the absence of females contributed to the intensity and duration of this wholly agonistic relationship. Support for this view may be found in the fact that the observations of Gill and Lanyon (1964) on the territorial behavior of male Blue-wings known to be mated, differed markedly from our bird. We saw practically none of the displays which they associated with territorial defense (i.e., Tail Pumping, Wing and Tail Flicks), and they apparently saw none of the more striking displays we observed. Since it is known that the songs of many warblers change after nesting begins (including pinus and chrysoptera), it could be expected that there are associative behavioral changes as well.

However, M. S. Ficken states (in litt.) that the "encounters may be more intense when females arrive, e.g. more fights than you observed, at least from our observations in somewhat comparable situations." She further suggests that the behavioral differences between Gill and Lanyon's (ibid.) Blue-wing/Blue-wing encounters and our Blue-wing/"Brewster's" encounters may be due to plumage differences: "From what we know of visual releasers, it might be expected that they [Blue-wings, Golden-wings and hybrids] would not react quite the same to a bird with another plumage. I have also found that in mixed pairings of Brewster's male and Blue-wing female, the male and female behaved differently toward each other than in conspecific pairings of Blue-wings."

It seems to us that all of these suggestions have merit, and to one degree or another may be applicable, but it is obvious that a better foundation of ethological understanding of these species will be required before such a complex set of interactions can be properly interpreted.

SUMMARY

One male Blue-winged Warbler and one male "Brewster's" Warbler were observed for 25 hours during a series of prolonged agonistic encounters. Aerial and non-aerial displays and vocalizations are described and illustrated. Morphologically, the Blue-wing and the "Brewster's" seemed "pure." The "Brewster's" sang a typical chrysoptera song. Two song types of the Blue-wing were more like chrysoptera than pinus. At the end of the observation period the "Brewster's" was confined to a very small part of its initially large territory, due, we believe, to the persistent aggressive behavior of the Blue-wing.

ACKNOWLEDGMENTS

We are indebted to Mrs. Jean Baxter for locating and calling to our attention the "Brewster's" Warbler. We also wish to thank Dr. Robert W. Ficken for providing us with sonograms of the songs, and Dr. Millicent S. Ficken for reading the manuscript and making many helpful suggestions.

APPENDIX

Maintenance behavior

In the course of our 25 hours of observation in 1961, we had several opportunities

to observe maintenance behavior in both the Blue-winged and the "Brewster's" Warbler. Due to the paucity of such information we would like to comment briefly on this behavior:

Head-scratching.—Indirect head-scratching was observed 9 times. During preening sessions the Blue-wing was seen to head-scratch twice and the "Brewster's" five times. Twice the "Brewster's" was seen to head-scratch without comfort movements preceding or following it.

Preening.—Both the Blue-wing and the "Brewster's" were observed preening several times. On each oceasion, preening was accompanied by such other comfort movements as head-scratching, wing-stretching, and tail-spreading. Preening was essentially the same in both birds (as illustrated by the following protocol): "preened breast feathers several times, preened seapular tract on both sides while drooping wing, preened flank and rump feathers. Shuffled body and wing feathers while spreading and shaking tail." Both birds were seen to preen while singing.

Stretching movements.—Only one stretching movement was observed (the wing and leg sideways stretch of Ficken, 1962b). The Blue-wing was seen during a preening session to stretch its left wing to the back and side (over its left leg?), while spreading tail. The "Brewster's" was seen to do the wing and leg sideways stretch several times.

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